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Evaluation of Lake Ontario salmonid niche space overlap using stable isotopes

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ABSTRACT

The Lake Ontario ecosystem has undergone substantial ecological change over the past five decades. In this time, an economically important sport fishery developed around non-native salmon and trout species (i.e., Chinook and coho salmon (*Oncorhynchus tshawytscha* and *Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*)). While trying to maintain this economically important recreational fishery, fishery managers are also trying to restore native species to the ecosystem (i.e., lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*)). We describe the trophic niche space of five ecologically and socioeconomically important Lake Ontario salmonid species (Chinook and coho salmon and rainbow, brown (*Salmo trutta*) and lake trout) using stable isotopes of carbon and nitrogen (^{13}C and ^{15}N, respectively). Using a modified standard ellipse analysis, we found a high degree of stable isotope niche space overlap in Lake Ontario salmonid species. Lake trout had the largest trophic niche space and the smallest proportion of overlap relative to the other four salmonid species (14%–28%), whereas coho salmon had the smallest stable isotope niche space and exhibited the highest degree of overlap with the other species (66%–99%). This study identifies and quantifies dietary resource sharing between Lake Ontario salmonids and highlights the importance of other prey fish species to the restoration and sustainability of Lake Ontario salmonid fish stocks.

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Introduction

The Lake Ontario ecosystem has undergone substantial ecological change over the past five decades. Numerous stressors, such as invasive species, fishery exploitation and eutrophication have contributed to the degradation of the Lake Ontario fish community (Mills et al., 2003). Since 1970 and the establishment of the Great Lakes Water Quality agreement in 1972, the negative effects of fish exploitation, sea lamprey (*Petromyzon marinus*), eutrophication and increasing alewife (*Alosa pseudoharengus*) abundances have been subdued, paving the way for the recovery and restoration of the Lake Ontario ecosystem. In this time, an economically important recreational sport fishery evolved around several non-native salmon and trout species (i.e., Chinook and coho salmon (*Oncorhynchus tshawytscha* and *Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*)) in Lake Ontario (Pearce et al., 1980). These predators were effective in controlling alewife populations, which through top-down effect, started to restore balance and stability in the lower trophic levels and ultimately the Lake Ontario food web (Mills et al., 2003).

Sea lamprey predation resulted in the extirpation of Lake Ontario lake trout (*Salvelinus namaycush*) in the 1950s and hindered the success of early salmonid stocking programs (Elrod et al., 1995; Schneider et al., 1983). In 1971, sea lamprey control began (Elrod et al., 1995) and in 1973 lake trout stocking was renewed in hopes of re-establishing a self-sustaining population (Schneider et al., 1983). In addition to lake trout, brown trout (*Salmo trutta*), rainbow trout, Atlantic salmon (*Salmo salar*), Chinook salmon and coho salmon were also stocked in an attempt to find the most suitable mixture of fish species for the lake. Chinook salmon were an attractive stocking species to both fishery managers and recreational anglers as they are a large, fast-growing salmon, that could consume large numbers of alewife, and have lower hatchery production costs (Mills et al., 2003). With the establishment of an annual $7 billion dollar recreational Great Lakes salmonid fishery (Dettmers et al., 2012), fishery managers find themselves trying to maintain the balance of supporting a diversity of salmon and trout dominated by trophy-sized Chinook salmon, and protection and restoration of native species (i.e., lake trout and Atlantic salmon) (Stewart et al., 2013).

Increasing the number of top predators in the offshore has led to an increasing need to understand how all of Lake Ontario's salmon and trout species (both native and non-native) are able to co-exist. Understanding the trophic ecology and interactions of the salmonid fishes in Lake Ontario will help resource managers identify potential for sustaining a large and diverse salmonid fishery without jeopardizing native species restoration or upsetting the predator–prey balance (Brenden et al., 2012; Murry et al., 2010; Stewart et al., 2013; Tsehaye et al., 2014). A food web characterizes dominant taxa and trophic interactions

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among prey and predators in an ecosystem. Food webs, including the relative importance of different linkages can change in response to ecological changes (e.g., prey die offs or environmental effects), making them dynamic by nature. Food webs can also be used to describe the trophic "niche" of a species (Jackson et al., 2011; Layman et al., 2007; Post et al., 2007). A species "niche" has been defined as the sum of all the interactions that link it to other species in an ecosystem. As such, a species niche is strongly connected to its position in the food web, and describing the niche accurately can be vital in identifying resource availability and subsequently, potential competition among species.

Traditionally, food webs were constructed using gut content data. The presence and relative dominance of prey found in the species stomach helped quantify the predator–prey interaction, and collectively these species associations defined the food web (Brandt, 1986; Hyslop, 1980). The benefit of this approach is the high resolution of prey identification that can occur, however, the stomach contents represent a small temporal "snapshot" of the predator's diet. Extensive diet analyses, spanning spatial and temporal scales reflective of the species behavior are needed to accurately characterize the species interactions. Stable isotopes can be used complementary to diet analyses, to provide a time integrated depiction of assimilated food, albeit at a lower level of taxonomic resolution. Stable isotopes of nitrogen (δ^{15}N; ratio of ^{15}N to ^{14}N) and carbon (δ^{13}C; ratio of ^{13}C to ^{12}C) are commonly used in food web ecology and are derived from all trophic pathways culminating in that individual; therefore, they can be used to depict trophic linkages in a food web as well as trophic niche (Jackson et al., 2011; Layman et al., 2007; Peterson and Fry, 1987; Post, 2002).

Layman et al. (2007) proposed six different metrics describing "community-wide" measures of trophic structure using stable isotope ratios. Four of the metrics (δ^{15}N range, δ^{13}C range, total convex hull area and mean distance to centroid) measure the total extent of spacing within isotope biplot space and the other two metrics reflect relative position of species to each other within trophic niche space and can be used to estimate the extent of trophic redundancy. The third metric proposed by Layman et al. (2007), total convex hull area (TA), represents the total area encompassed by all individuals of a species in δ^{13}C–δ^{15}N biplot space. It represents a measure of the total amount of trophic niche space occupied, allowing inferences to be made surrounding the total extent of trophic diversity within a food web. The metrics proposed by Layman et al. (2007) moved the analysis and interpretation of stable isotope food webs from qualitative to quantitative. Most of the attention has revolved around the use of TA to describe the trophic niche width of an organism or community (Layman et al., 2007; Quevedo et al., 2009); however there are some disadvantages to using this metric.

One disadvantage to using the TA metric proposed by Layman et al. (2007) is that the metric is sensitive to sample size (Hoeinghaus and Zeug, 2008; Jackson et al., 2011). This is less than ideal where sample sizes differ among samples within studies, or when comparisons across multiple studies are conducted. Jackson et al. (2011) proposed the use of standard ellipses (Batschelet, 1981) to describe and make inference on isotopic niche space, instead of using convex hulls and other extreme value metrics. The advantage of this method is that the effect of small sample sizes on the standard ellipses is reduced (Batschelet, 1981); furthermore, Jackson et al. (2011) have provided an alternative sample size correction for the standard ellipses, allowing for robust meta-analyses between studies that contain different sample sizes. Both papers by Layman et al. (2007) and Jackson et al. (2011) provide ecologists with tools to help discern and describe key factors driving community structure.

This study is the first to describe the isotopic trophic niche space of the Lake Ontario salmonid community. With growing public concern surrounding potential competition among salmonid species (i.e., lake trout and Chinook salmon), including efforts to rehabilitate native salmonids (Atlantic salmon and lake trout), we use the standard ellipse (Batschelet, 1981) approach proposed by Jackson et al. (2011) to evaluate the extent of isotopic trophic niche overlap (hereafter referred to as niche overlap) within the Lake Ontario salmonid community.

Methods

Sample collection

Eight hundred twenty salmonids were sampled from multiple sites throughout Lake Ontario using either bottom-set, graded-mesh gillnets (50-m panels of 38- to 151-mm monofilament mesh in 12.7-mm increments) or from tissues taken from angler caught fish using a biopsy punch. At each sampling location (Table 1), three or four nets were set parallel to depth contours beginning at the 10 °C isotherm, rarely shallower than 25 m, and proceeding in 10 m depth increments to a maximum of 50 m (Rush et al., 2012). The angler caught fish were sampled during routine Ontario Ministry of Natural Resources (OMNR) Lake Ontario creel surveys during which interviewed anglers were asked to volunteer their catch for tissue sampling. Using a Unicore 3.5 mm biopsy punch (Ted Pella Inc., Redding, CA), skinless boneless dorsal muscle tissue was extracted from each fish and placed in a storage vial. Between sampling each fish, the biopsy needle was sterilized in bleach and rinsed in distilled water to prevent cross contamination of tissue samples. The use of the biopsy needle to sample angler fish proved to be quite successful and provided 92 tissue samples from five salmonid species that are not easily accessible through traditional netting techniques (Ontario Ministry of Natural Resources, 2013). Initially vials were held in coolers on ice until they could be moved to −20 °C freezer for storage. All tissue samples were freeze-dried in cryotubes for 48 h and homogenized with a glass rod prior to stable isotope analyses.

Stable isotope analysis

For tissues collected from 2008 to 2012 Rush et al. (2012) give details of stable isotope tissue preparation. Briefly, stable isotope analyses were completed using lipid-extracted (LE) sample preparations (chloroform–methanol extraction, Bligh and Dyer, 1959). Tissue samples collected between 2009 and 2011 were not lipid extracted prior to stable isotope analysis. To facilitate comparisons, results for these samples were adjusted using sample carbon/nitrogen ratios (Boecklen et al., 2011; Post et al., 2007). Stable isotope analyses were completed using a Delta Plus isotope-ratio mass spectrometer (Thermo Finnigan, San Jose, CA, U.S.A.) coupled with an elemental analyzer (Costech, Valencia, CA, U.S.A.). Values of δ^{13}C and δ^{15}N were quantified in relation to three internal laboratory standards and an NIST standard (#8414 bovine muscle), which was run every 12 samples. Atmospheric nitrogen and Vienna Pee Dee Belemnite carbonate were the standard reference materials for ^{15}N and ^{13}C respectively. The analytical precision based on the standard deviation of reference standards, which were ±0.05‰ for δ^{13}C and ±0.12‰ for δ^{15}N for NIST standard 8414 ($n = 207$), and ±0.12‰ for δ^{13}C and ±0.17‰ for δ^{15}N for an internal fish muscle standard ($n = 214$). Standard deviations of replicate samples were ±0.24‰ for δ^{13}C and ±0.18‰ for δ^{15}N ($n = 179$). All stable isotope analyses on 2008 to 2012 tissues were completed by the Chemical Tracers Laboratory at the University of Windsor's Great Lakes Institute for Environmental Research.

Statistical analyses

Due to the small sample size of small fish (22 of 886 < 300 mm fork length), only large fish were considered in our analyses. This effectively removed strong ontogenetic effects, known to occur with these salmonid species. As our data came from multiple years, we used an ANOVA to test whether stable isotope values for each species changed through time. If year was not a significant effect, the data were pooled.

To examine stable isotope niche overlap, we followed the methods outlined in Jackson et al. (2011) using standard ellipses (Batschelet,

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Table 1
Port locations for bottom-set, graded-mesh gillnets Latitude and longitude coordinates are provided in degree minutes seconds (DMS).

Country	Prov./state	Port	Latitude (DMS)	Longitude (DMS)
Canada	Ontario	Grimsby	43°11′39.17″	79°33′44.71″
Canada	Ontario	Bronte	43°23′50.55″	79°42′46.71″
Canada	Ontario	Oshawa	43°53′49.53″	78°51′56.85″
Canada	Ontario	Flatt Point	43°56′21.07″	76°54′32.23″
Canada	Ontario	Eastern Basin	43°52′35.94″	76°58′26.24″
Canada	Ontario	North East Channel	44°02′44.05″	76°24′36.84″
United States	New York	Southwick	43°45′55.66″	76°11′55.35″
United States	New York	Oswego	43°27′19.25″	76°30′37.79″
United States	New York	Fall Haven	43°12′32.52″	77°24′42.12″
United States	New York	Sodus	43°14′16.23″	77°03′40.90″
United States	New York	Pultneyville	43°16′47.23″	77°11′09.93″
United States	New York	Smokey Point	43°15′33.08″	77°27′01.88″
United States	New York	Rochester	43°15′02.72″	77°37′00.48″
United States	New York	Hamlin	43°21′08.38″	77°53′27.83″
United States	New York	Oak Orchard	43°21′30.08″	78°11′51.34″
United States	New York	30-Mile Point	43°22′20.97″	78°28′15.97″
United States	New York	Olcott	43°18′59.87″	78°43′34.63″
United States	New York	Niagara Bar	43°18′57.01″	78°50′18.71″

1981) with a slight modification. We felt that the standard ellipse analysis proposed by Jackson et al. (2011) was too restrictive (mean ± 1 standard deviation) and instead used two standard deviations as proposed by Stasko (2012) to encompass a greater proportion of each species population. Corrected standard ellipse areas (SEA_{Ec}) were used to compensate for species with small sample sizes (Jackson et al., 2011).

A Bayesian iterative process was used to create multiple estimates of SEA_{Ec} and evaluate the relative sizes of the ellipses based on their respective sample sizes. This process creates a SEA_{Ec} estimate for each species based on a subsample of the population's stable isotope values (Jackson et al., 2011). These values were then used to estimate the proportion of SEA_{Ec} of one salmonid species that are smaller than another species. This process accounts for uncertainty in the sampled data and provides essential information surrounding the relative size of each stable isotope niche space relative to each species examined (Jackson et al., 2011).

All statistical analyses were conducted in R (R Core Team, 2014) using the car (Fox and Weisberg, 2011), multcomp (Hothorn et al., 2008) and Stable Isotopes Analysis in R (SIAR — Parnell et al., 2010) packages.

Results

A total of 820 salmonids were analyzed for stable isotopes of ^{13}C and ^{15}N (Table 2). With the exception of coho salmon, which were only collected in 2012, differences in stable isotope values (δ^{13}C and δ^{15}N) between years for each species were detected (Chinook salmon: ANOVA on δ^{13}C and δ^{15}N, $p < 0.01$ for both, $F_{2,118} = 7.772$ and 15.29; rainbow trout: ANOVA on δ^{13}C, $p = 0.04$, $F_{1,31} = 4.819$; brown trout: ANOVA on δ^{13}C, $p < 0.01$, $F_{3,67} = 10.09$; lake trout: ANOVA on δ^{13}C, $p < 0.01$, $F_{5,569} = 6.502$). While these comparisons of δ^{13}C and δ^{15}N among years revealed statistically significant differences, the differences between maximum and minimum isotope values among years were small (maximum 0.85‰ for δ^{13}C of brown trout and maximum 0.54‰ for δ^{15}N of Chinook salmon). As a result, stable isotope data for each species were pooled across all years for isotope niche space analyses.

Isotope niche space analyses found lake trout had the largest SEA_{E}, SEA_{Ec} and convex hull followed by brown trout, rainbow trout, Chinook salmon and coho salmon (Fig. 1; Table 3). Lake trout had the highest sample size ($n = 575$) relative to the other four species. To test the effect of sample size on the SEA_{Ec}, a subsample of 20 individual lake trout was taken 1000 times (with replacement) and SEA_{Ec} was calculated. The mean SEA_{Ec} from subsampling was not significantly different than the SEA_{Ec} calculated using all 575 individuals (Student's t-test, $p < 0.001$; 0.6% difference between the values). Bayesian ellipse analysis (Jackson et al., 2011) provides some insight into the relative SEA_{Ec} size of each salmonid species (Table 4). Based on this analysis, lake trout continued to have the largest SEA_{Ec} relative to the other salmonids, followed by rainbow trout, brown trout, coho salmon and Chinook salmon. The relative ellipse sizes (largest to smallest) are different than those determined using SEA_{Ec} with the full dataset (Tables 3 and 4). This discrepancy is likely a result of smaller sample sizes (Table 2) and possible ontogenetic effects on rainbow trout (despite the fork length restriction of 300 mm). Despite the differences, the same general pattern of relative size is maintained.

The overlap analysis for the salmonid stable isotope niche space revealed that the coho salmon niche space was shared (from 66% with rainbow trout to 100% with brown trout) with all of the other salmonids (Table 5 and Fig. 1). Chinook salmon had the second highest level of niche overlap from 44% with coho salmon up to 99% with brown trout

Table 2
Biological data on the five Lake Ontario salmonid species. Sample size (n), fork length (FLEN; mean ± SD (min, max)), δ^{13}C (mean ± SD), δ^{15}N (mean ± SD), C:N (mean ± SD) and data source. [1]T. Johnson, OMNR unpublished data; [2]Rush et al., 2012; [3]T. Stewart, OMNR unpublished data.

Species	n	FLEN ± SD (mm) (min, max)	δ^{13}C ± SD (‰)	δ^{15}N ± SD (‰)	C:N ± SD	Source
Coho salmon	20	639 ± 34 (570, 720)	−22.34 ± 0.23	15.82 ± 0.28	3.34 ± 0.21	1
Chinook salmon	121	588 ± 204 (300, 970)	−22.07 ± 0.37	15.61 ± 0.42	3.48 ± 1.11	1, 3
Rainbow trout	33	579 ± 118 (370, 800)	−22.00 ± 0.28	15.32 ± 1.01	3.33 ± 0.40	1
Brown trout	71	525 ± 62 (340, 680)	−21.90 ± 0.68	15.52 ± 0.45	4.11 ± 0.87	1
Lake trout	575	634 ± 143 (300, 950)	−22.53 ± 0.56	16.98 ± 0.75	4.98 ± 1.35	1, 2

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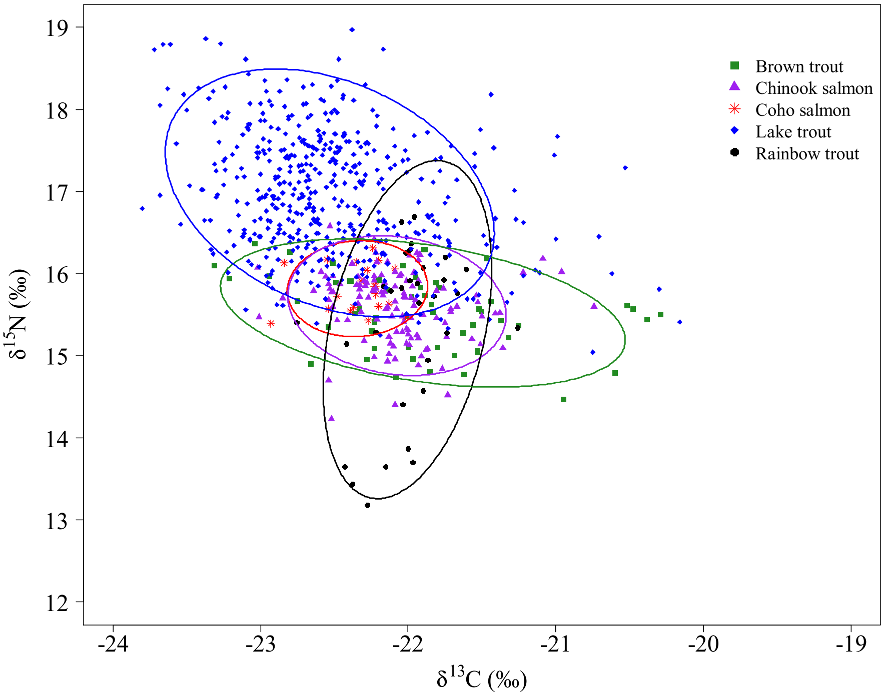

Fig. 1. Expanded standard ellipse (SEA_{Ec}) isotope niche space of five Lake Ontario salmonid species. Standard ellipses were created following methods outlined in Batschelet (1981) but expanded to incorporate two standard deviations (Stasko, 2012) in contrast to one standard deviation as used in Jackson et al. (2011).

(Table 5 and Fig. 1). Rainbow and brown trout had a moderate amount of overlap sharing from 17% and 24% with coho salmon (respectively) and 48% and 46% with each other (respectively; Table 5 and Fig. 1). Contrary to our expectations, lake trout had the least amount of stable isotope niche overlap, sharing from 14% with coho salmon to 28% with rainbow trout (Table 5 and Fig. 1).

Discussion

The current study has depicted the stable isotope trophic niche space of five Lake Ontario salmonids. Coho salmon have the smallest trophic niche space followed by Chinook salmon, brown trout, rainbow trout and finally lake trout. Trophic niche space analyses offer insight into resource use of both individual species and overlap among species. However, caution should be taken as the seasonal distribution of both predator and prey, as well as their respective habitat uses need to be understood for proper interpretation of niche space analysis.

Coho and Chinook salmon have the smallest trophic niche spaces of the five salmonids examined in this study (Fig. 1). This implies that both species have a narrow prey base, which based on previous studies (Brandt, 1986; Jacobs et al., 2013; Olsen et al., 1988), is likely dominated by Lake Ontario's most abundant pelagic prey fish, alewife. Additionally, alewife stable isotope values are less variable than other prey sources (e.g., rainbow smelt (*Osmerus mordax*), sculpin spp., round goby (*Neogobius melanostomus*)) available to these salmonids (Rush et al., 2012; Yuille et al., 2012). A predator feeding on one prey item, such as round goby, which has a more diverse diet reflected in their stable isotope values (Brush et al., 2012; Rush et al., 2012; Yuille et al., 2012), would have a larger trophic niche space than a predator feeding on one prey item, such as alewife, which exhibits smaller amounts of variation in their stable isotope values. Thus, the small trophic niche spaces of Coho and Chinook salmon are likely further exacerbated by the limited amount of isotopic variation in their prey population. Brown trout are feeding on a variety of prey sources within the same trophic level (narrow $\delta^{15}N$ range) but spanning both the pelagic and littoral habitats (wide $\delta^{13}C$ range). In contrast, rainbow trout are feeding through multiple trophic levels (wide $\delta^{15}N$ range) within a narrow spatial scale (narrow $\delta^{13}C$ range). The range in $\delta^{15}N$ with size is consistent with the ontogenetic feeding of the species, reflecting the shift from a diet dominated by invertebrates to mainly piscivory (Scott and Crossman, 1990). Contrary to our expectations, lake trout had the largest trophic niche space and the smallest proportion of isotope niche overlap relative to the other four species, which suggests that the trophic ecology of lake trout is the most unique among the salmonid species examined. Brandt (1986) estimated food resource overlap greater than 70% between lake trout and other salmonids; however our study indicated a maximum overlap less than 30% (Table 5). Lake Ontario has undergone dramatic ecosystem change since the studies by Brandt (1986) and

Table 3
Stable isotopic area (‰^{2}) encompassed by: expanded standard ellipse area (SEA_E, 2 standard deviations from the centroid) representing two standard deviations as does the corrected expanded standard ellipse area (SEA_{Ec}; ellipse adjusted for small sample sizes) and total convex hull area (TA; isotopic area encompassed by connecting the outermost species isotope values) for five Lake Ontario salmonid species.

Species	SEA_E (‰^{2})	SEA_{Ec} (‰^{2})	TA (‰^{2})
Coho salmon	0.824	0.870	0.648
Chinook salmon	1.937	1.954	3.458
Rainbow trout	3.333	3.448	2.823
Brown trout	3.548	3.617	3.676
Lake trout	4.981	4.992	10.592

Table 4
The proportion (%) of SEA_{Ec} from species listed in the rows that are smaller than the SEA_{Ec} of species listed in the columns.

	Coho salmon	Chinook salmon	Rainbow trout	Brown trout	Lake trout
Coho salmon	–				
Chinook salmon	54.20	–			
Rainbow trout	0.43	0.00	–		
Brown trout	1.64	0.00	80.92	–	
Lake trout	0.08	0.00	44.62	6.39	–

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Table 5
Proportion (%) of SEA_{Ec} overlap between salmonid species in the row against salmonid species in the column; information illustrated in Fig. 1.

	Coho salmon	Chinook salmon	Rainbow trout	Brown trout	Lake trout
Coho salmon	–	44.25	16.67	24.06	13.83
Chinook salmon	99.36	–	44.69	53.34	19.37
Rainbow trout	66.07	78.87	–	45.62	28.45
Brown trout	99.99	98.75	47.85	–	23.53
Lake trout	79.32	49.48	41.18	32.48	–

Olsen et al. (1988), which may have resulted in fundamental shifts in lake trout diets (Mills et al., 2003; Rush et al., 2012). Two such changes include the establishment of dreissenid mussels and establishment of round goby populations in the lake (Mills et al., 2003). Round goby, a non-native benthivorous fish from the Ponto–Caspian region of Eastern Europe, were first discovered in Lake Ontario in 1998 (Mills et al., 2003). Since then, round goby abundance and distribution have increased. With the loss of their native prey species (*Coregonus* spp.) in the 1970s (Mills et al., 2003), lake trout consumed alewife (Brandt, 1986; Olsen et al., 1988), however, the size of their stable isotope trophic niche space suggests that their diet is diverse, consisting of more than just alewife.

To decrease the amount of stable isotope trophic niche overlap, lake trout must be consuming higher proportions of other prey fish species such as, rainbow smelt, sculpin (Brandt, 1986; Olsen et al., 1988), round goby, or even other smaller lake trout (Dietrich et al., 2006; Rush et al., 2012). Lake trout are known to be cannibalistic (Martin, 1970; Dietrich et al., 2006), which could contribute to the elevated $\delta^{15}N$ of the lake trout stable isotope trophic niche space. Dietrich et al. (2006) showed that the diets of lake trout greater than 450 mm in fork length could consist of up to 21% by mass (g) of smaller lake trout. In addition, round goby have expanded their distribution to deeper depths in the lake and may also be playing a larger role in lake trout diets than once suspected (Dietrich et al., 2006; Rush et al., 2012). Stable isotope values for Lake Ontario round goby caught deeper than (>15 m) are significantly higher in $\delta^{15}N$ and more depleted in $\delta^{13}C$ relative to nearshore (<15 m) round goby (OMNR unpublished data) suggesting that the possibility of round goby inhabiting deeper depths could be contributing a significant portion to lake trout diets. In addition, slimy sculpin (*Cottus cognatus*) and deepwater sculpin (*Myoxocephalus thompsonii*) had contributed to lake trout diets historically (Christie et al., 1987; Rand and Stewart, 1998), but with the establishment of alewife and smelt in the lake, densities of sculpin decreased (Christie et al., 1987; Mills et al., 2003). Recently, deepwater sculpin abundances have increased (Ontario Ministry of Natural Resources, 2013) and may once again be diversifying the diet of lake trout. As a demersal top predator, the availability of these benthic prey fish to lake trout could enlarge their trophic niche and provide lake trout with some dietary flexibility to exploit prey that are used less by other salmonids.

In general, the highest degree of overlap between these species occurs in limited isotope space: between −23‰ and −22‰ $\delta^{13}C$ and between 15‰ and 16.5‰ $\delta^{15}N$, which suggests that there is a common prey source that is driving the observed overlap. Tissue-diet fractionation is minimal for carbon, but typically the $\delta^{15}N$ values of predators are enriched relative to their prey following a narrowing discrimination-scaled framework (Hussey et al., 2014). Previous studies have shown that Lake Ontario alewife have $\delta^{15}N$ and $\delta^{13}C$ values between 12‰ and 14‰ and −24‰ and −22‰ respectively (Rush et al., 2012; Yuille et al., 2012), suggesting that alewife may be a common prey resource driving the trophic niche overlap between all salmonids observed in this study. Similarly, Lake Ontario rainbow smelt and slimy sculpin are higher in $\delta^{15}N$ and more depleted in $\delta^{13}C$ relative to alewife (Rush et al., 2012), suggesting that lake trout may be incorporating these prey fish in their diet, contributing to their high proportion of non-overlapping trophic niche space with other salmonids (Fig. 1).

While the degree of overlap among isotopic trophic niche space might imply intensity of competition, such interpretation must be made cautiously as our results do not reflect relative abundance of the prey or predator or the seasonal and spatial distributions of these salmonids. Liem's Paradox suggests that feeding specialists may act primarily as generalist feeders in nature, which can create a mismatch between diet and morphology (Robinson and Wilson, 1998). Robinson and Wilson (1998) explain that phenotypic specialists can function as ecological generalists because some resources are intrinsically easy to use, even by consumers that have evolved specialized traits to exploit less-favored resources. In the case of Lake Ontario, alewife dominate the prey fish community (Ontario Ministry of Natural Resources, 2013), however comparisons with other species are difficult due to current survey methodology. While slimy sculpin dominated the bottom trawl catch prior to 2004, round goby now comprise >75% of the biomass, with deepwater sculpin representing approximately 10% of the biomass since 2011 (B. Weidel, USGS, Oswego, unpublished data). Owing to the high abundance of alewife and their isotopic alignment with many of the predator trophic niche spaces, we might expect alewife to dominate the diet of many of the salmonid predators in Lake Ontario, which previous diet studies suggest (Brandt, 1986; Lantry, 2001; Olsen et al., 1988). If this prey source becomes less abundant, decreasing its “ease of use”, Lake Ontario salmonid trophic niche spaces may become more individualized on a species basis, as each species feeds on and exploits the “less-favored” resources for which they are well adapted (Liem and Kaufman, 1984; Robinson and Wilson, 1998).

Using $\delta^{13}C$ stable isotopes can provide an indication of spatial habitat related to the predator feeding, with more ^{13}C-depleted values suggesting pelagic carbon sources and more ^{13}C-enriched values indicating more littoral carbon sources (Hecky and Hesslein, 1995). Thus, the $\delta^{13}C$ overlap in stable isotope trophic niche space implies similar prey sources and indicates overlap along a nearshore-to-offshore spatial continuum (Jackson et al., 2011; Layman et al., 2007). However, this does not provide any information on depth distribution. Previous studies on salmonid resource partitioning suggest that while some salmonid species (i.e., brown trout, lake trout and Chinook salmon) have similar diets, they obtain their prey from different spatial areas (depths) of the lake (Olsen et al., 1988). This cannot be discerned from the stable isotope plots as we cannot infer salmonid depth distribution from the $\delta^{13}C$ and $\delta^{15}N$ biplot. However, depth distribution data has shown that large alewife, rainbow smelt and slimy sculpin (age 1+) have moved to deeper waters in the mid-1990s (O'Gorman et al., 2000; USGS, Oswego, NY, unpublished data), while smaller alewife and rainbow smelt (young-of-year) are found in the epilimnetic and metalimnetic waters (respectively, Ontario Ministry of Natural Resources, 2013). Thus, the diets of these salmonids could be dominated by alewife, but each species may be exploiting the resource within their own thermal (and subsequently depth) optima. Furthermore, the stable isotope values of the same species of prey fish may change with depth and temperature. Peterson and Fry (1987) suggest that $\delta^{15}N$ can increase 5–10‰ as depth increases, supporting the idea that lake trout may be eating the same prey species (alewife) as other salmonids but at a deeper depth strata, which has elevated their overall stable isotope trophic niche relative to the other salmonids. Such resource partitioning through spatial separation is necessary in ecosystems where there is a high degree of sympatry, allowing potential competitors to coexist (Olsen et al., 1988; Schoener, 1974). The overlap observed in biplot space may dissolve if depth and temperature data were incorporated into the plot. For the proper analysis, the feeding depth of the salmonids needs to be incorporated into the analysis.

From this analysis, inferences can be made about the ability of a species or population to respond to environmental change. Feeding generalists will have larger stable isotope trophic niche ellipses that span a range of both ^{15}N and ^{13}C (i.e., lake trout), whereas specialists are represented by smaller ellipses (i.e., coho salmon) restricted in ^{15}N and ^{13}C. Ellipse size will reflect the ability of each species to change their diet,

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thus, food web disruptions will affect species with large and small ellipses differently (Jackson et al., 2011; Layman et al., 2007). For example, coho salmon have a very restricted prey base; a collapse of a single prey fish species could be detrimental to the success of their population. In contrast, the collapse of that same prey species suggests that lake trout would be minimally affected, as their large ellipse implies that the population relies on multiple food sources and would be more likely to shift their prey base in response to the prey fish collapse. When alewife populations in Lake Huron declined, coho and Chinook salmon abundances also declined (Riley, 2013). However, other salmonid species not only appeared to be unaffected (i.e., lake trout), but their natural reproduction also increased (Riley, 2013). Thus, stable isotope niche analyses can be used to identify species that are sensitive or robust to dynamic food resources.

Overall, there is a great degree of stable isotope trophic niche overlap with Lake Ontario salmonid species. This is likely driven by alewife consumption as it is the dominant prey fish in the lake. Lake trout stable isotope values were more diverse than expected, resulting in the largest stable isotope niche space. Furthermore, lake trout had the least amount of trophic niche overlap relative to the other salmonid species. Again, the observed overlap between lake trout and the other salmonids is likely a product of alewife consumption, however further investigation is needed to explain the diversity of lake trout diets. Both the lack of stable isotope niche overlap between prized recreational fish (e.g., Chinook salmon) and the native top predator (i.e., lake trout) and the abundance of prey fish species (e.g., alewife and round goby) suggest that competition between these species for food resources is low. However, this study has revealed essential questions in need of answering. The stable isotope niche space of juvenile and young-of-year salmonids (<300 mm fork length) needs to be examined. Data on this salmonid life stage are sparse as anglers do not target fish in this size range and their catchability in community indexing gear is low (Ontario Ministry of Natural Resources, 2013). It is essential to characterize these younger salmonid stages as their success directly influences the sustainability of these species. In addition, research needs to be conducted to determine both nearshore/offshore as well as depth differences in prey fish stable isotope values. With the addition of diet data and prey source isotope data, stable isotope mixing models (e.g., MixSIR) could be used to help infer isotope sources of top predators, helping to identify which prey species are driving the observed stable isotope niche overlap. This will shed light on whether salmonids are consuming the same prey fish but in separate spatial regions, or if the predators are consuming completely different prey fish. While looking at other systems where alewife populations collapsed (i.e., Lake Huron) helps us to infer predicted changes in Lake Ontario, future studies should examine Lake Ontario salmonid stable isotope niche overlap from historic scale data when alewife abundances were low (i.e., throughout the 1990s) to determine whether the overlap observed in this study is real or artificial (due to over-abundance of alewife). This study has not only helped to identify resource sharing between Lake Ontario salmonids, but also highlights the importance of other prey fish species (e.g., round goby and sculpin spp.) to the restoration and sustainability of Lake Ontario salmonid fish stocks.

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